



Extreme weather events threaten biodiversity and functions of river ecosystems: evidence from a meta-analysis

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ABSTRACT

Both gradual and extreme weather changes trigger complex ecological responses in river ecosystems. It is still unclear to what extent trend or event effects alter biodiversity and functioning in river ecosystems, adding considerable uncertainty to predictions of their future dynamics. Using a comprehensive database of 71 published studies, we show that event – but not trend – effects associated with extreme changes in water flow and temperature substantially reduce species richness. Furthermore, event effects – particularly those affecting hydrological dynamics – on biodiversity and primary productivity were twice as high as impacts due to gradual changes. The synthesis of the available evidence reveals that event effects induce regime shifts in river ecosystems, particularly affecting organisms such as invertebrates. Among extreme weather events, dryness associated with flow interruption caused the largest effects on biota and ecosystem functions in rivers. Effects on ecosystem functions (primary production, organic matter decomposition and respiration) were asymmetric, with only primary production exhibiting a negative response to extreme weather events. Our meta-analysis highlights the disproportionate impact of event effects on river biodiversity and ecosystem functions, with implications for the long-term conservation and management of river ecosystems. However, few studies were available from tropical areas, and our conclusions therefore remain largely limited to temperate river systems. Further efforts need to be directed to assemble evidence of extreme events on river biodiversity and functioning.

Key words: flow interruption, floods, temperature, species richness, abundance, river ecosystem.

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I. INTRODUCTION

Extreme weather events are becoming more frequent and unpredictable as global warming and human activities jointly alter the water cycle (Evans & Boyer-Souchet, 2012; Ummenhofer & Meehl, 2017; Best & Darby, 2020). Changes in rainfall and temperature patterns have led to prolonged heatwaves, abrupt decreases in water flow, or large floods, which are subsequently altering temporal patterns of water flow in river networks over large areas of the Earth (Messenger *et al.*, 2021). Low water flow periods have become longer (Döll & Zhang, 2010) and, as a result, river systems experience progressively stronger transitions towards slow-flowing phases (Sabater, 2008) or are completely interrupted (Messenger *et al.*, 2021). Furthermore, these hydrological changes have altered sedimentological processes (Inman & Jenkins, 1999), and increased water temperatures (Morrill, Bales & Conklin, 2005; Kaushal *et al.*, 2010). At the other extreme of hydrological events, large floods have become more frequent (Hirabayashi *et al.*, 2013; Arnell & Gosling, 2016), and already produce long-term effects in larger rivers of the world (e.g. Espinoza *et al.*, 2022). Large floods may transform the geomorphological setting of river networks and, when catastrophic, produce long-lasting impacts on river biodiversity (Woodward *et al.*, 2015). Thus the type and intensity of extreme events, principally hydrological and climatic events, likely affect the biodiversity and ecosystem functioning of river ecosystems, yet the magnitude and direction of their impacts remain to be comprehensively synthesized.

Extreme events, which frequently overlap in time and space (Bowler *et al.*, 2020), vary in their impacts on biodiversity and ecosystem functions (Rillig *et al.*, 2019). Ecosystems impacted by frequent disturbances, such as river networks, host ecological communities and provide ecosystem functions that respond directly to water flow patterns (Thorp, Thoms & Delong, 2006). River systems are increasingly affected by gradual changes (*trend effects*) and extreme events (*event effects*; Jentsch, Kreyling & Bejerkuhnlein, 2007) in their hydrology and climate patterns. While gradual changes in water flow and temperature can be classified as press disturbances, extreme events are equivalent to pulse disturbances (Lake, 2000; Harris *et al.*, 2018). The impacts of press disturbances on biodiversity may be seen as continuous and gradual, leading to shifts in species distributions and community structure (e.g. Mantua, Tohver & Hamlet, 2010). The pace of changes due to press disturbances may allow for some

degree of adaptation, at least for some species (Benedetti-Cecchi *et al.*, 2006; Heino, Virkkala & Toivonen, 2009). By contrast, the impacts of pulse disturbances may lead to abrupt changes in environmental conditions, disproportionately affecting species with limited opportunities for adaptation (Harris *et al.*, 2018; Ledger & Milner, 2015).

Press or pulse disturbances may differentially affect the capacity of ecosystems to resist and recover structurally and functionally (Jentsch & White, 2019). Changes to community structure due to trend and event effects may cascade to ecosystem functions, with unknown consequences for biodiversity–ecosystem function relationships (Biggs *et al.*, 2020). In terrestrial ecosystems such as experimental grassland communities, biodiversity consistently buffers variation in ecosystem functioning (productivity) for both extreme wet and dry events (Isbell *et al.*, 2015). Functional redundancy, i.e. the extent to which multiple species perform similar roles in a community, may moderate the impacts of extreme climate events on ecosystem functions (Woodward *et al.*, 2015). Quantifying the relative importance of the impacts of trend- and event-driven disturbances on biodiversity and ecosystem functions of river ecosystems is essential for developing data-driven adaptation and mitigation strategies.

Herein we perform a comprehensive meta-analysis that evaluates the relative impacts of trend and event weather effects on the biodiversity and ecosystem functions of river ecosystems. We compiled a database of 199 effect sizes, including both observational and experimental studies, to determine whether: (i) event effects have stronger, negative impacts than those of trend effects on diversity, abundance, and biomass of river communities, based on the assumption that pulse effects are stronger than press effects; (ii) hydrological anomalies lead to stronger or weaker impacts than temperature anomalies on river ecosystems; (iii) the impacts of trend and event effects on ecosystem functions (decomposition, respiration, primary production) are weaker than impacts on biodiversity, since ecosystem functions may be maintained at pre-disturbance levels where functional redundancy is high.

II. METHODS

(1) Data collection

We used the *Web of Science* and *Scopus* databases to perform a comprehensive search of relevant studies (Gusenbauer & Haddaway, 2020). Entries up to March 2021 were included using a composite search string with hydrological and

climatic descriptors considering different ecological communities and functions of river ecosystems (the complete set of Boolean terms is provided as online supporting information in Appendix S1). Our search returned 30,847 references, which was reduced to 1,235 unique records after removing duplicates (PRISMA diagram, Appendix S2). We only retained peer-reviewed papers testing the effects of climate change on biodiversity or ecosystem functions. These papers had to use standardized sampling methods (in the field or the laboratory), with at least one control and impact treatment and more than three samples for each. We included species richness, density (number of individuals per unit area), and biomass as descriptors of biodiversity, while organic matter decomposition, respiration, and primary production were included as descriptors of ecosystem functions (Hooper *et al.*, 2012).

We extracted mean values, standard deviations, standard errors, and the number of samples in control and impact treatments from tables, text, or figures. If the mean abundance or standard deviation were not reported, we derived these from the total abundance, sample size, and standard error, if possible. Data from figures were extracted using Webplot Digitizer 3.4 (Rohatgi, 2015). We also retrieved information on four moderators that we anticipated could affect biodiversity and ecosystem functions (Table S1). Following the information provided by the authors, for each extracted data point we collected information on the ecological community, type of effect (trend or event), anomaly type (increase or decrease in water flow; increase or decrease in water temperature), and study type (experimental or observational).

In total, we built a database of 199 effect sizes from 71 studies (each observational or experimental treatment was considered as a replication unit), of which only 21 had both biodiversity and ecosystem function data. All studies included in the meta-analysis are identified in the reference list with an asterisk. Effect sizes were calculated as standardized mean differences (Hedges' g) using means, standard deviations, and sample sizes retrieved from each study. We used the *escalc* function in the *metafor* package in R (Viechtbauer, 2010) to compute Hedges' g and its respective variance. To account for differences in sampling variance, we weighted the estimated effect sizes by their sample size as recommended by Hamman *et al.* (2018). Effect sizes are presented as units of the pooled standard deviation, such that a value of 0.5 represents a difference equivalent to half of a standard deviation. Thus, negative values indicate that climate change, whether trend or event, had a negative impact on the variables, while positive values indicate the opposite. The complete list of data sources, effect sizes, and moderators is available at <https://doi.org/10.5281/zenodo.7004412>.

(2) Data analysis

We used hierarchical Bayesian models to analyse variation in effect sizes, as implemented in the *brms* package in R (Bürkner, 2017). To distinguish between the effect of trend

versus event effects and the anomaly type, we fitted a univariate model for each predictor variable, excluding the intercept. We chose this approach because intercept models for categorical predictors with more than two levels use only one as the reference against all others (Doherty *et al.*, 2020). We considered predictor variables important for all models when the 95% credible intervals (CIs) of the posterior estimates did not overlap with zero. We did not evaluate interactions between fixed effects because some combinations of variables (e.g. extreme temperature decrease) were poorly replicated. We ran four chains of 10,000 iterations each for each model, with a burn-in of 1000 iterations, resulting in a total of 36,000 samples. We assessed convergence by inspecting trace plots and ensuring that the Gelman–Rubin statistic was <1.1 (Gelman & Rubin, 1992).

We specified non-informative normal priors ($\mu = 0$, $\sigma = 10$) for the fixed effects and weakly informative half Cauchy priors ($\mu = 0$, $\sigma = 1$) for the random effects (Bürkner, 2018). We fitted models assuming a normal distribution and included random effects for the study identity, type, and duration to account for non-independence between effect sizes from the same study or study type. By incorporating these categorical factors as random effects, we assume that the biodiversity and ecosystem function responses will be more similar within the same study (ID) and similar types of study (observational or experimental). To identify an appropriate structure of random effects, we fitted and ranked five nested models containing different combinations of study ID and type as random effects. The ecological community could not be included as a random effect factor because the number of samples per class was highly unbalanced. Model ranking using leave-one-out cross-validation (Vehtari, Gelman & Gabry, 2017) indicated different random effects structures for each response variable (Table S2).

To avoid potential confounding effects of unusually adverse events, we decided to exclude data points falling outside the ranges of the biodiversity (-10.3 to 9.1) and ecosystem function (0.04 to -7.7) aspects. These ranges accounted for the 1st percentile of the distribution of effect sizes in biodiversity (effect sizes less than -10) and ecosystem function variables (effect sizes less than -7). Specifically, we did not include some of the results from Romero *et al.* (2019) and Truchy *et al.* (2020) (Hedges' g for biomass between -14 and -244), Geraldes, Pascoal & Cassio (2012) (Hedges' g for decomposition greater than -10), and Oprei, Zlatanovic & Mutz (2019) (Hedges' g for respiration greater than -10). The inclusion of these studies increased the magnitude of the effect size for extreme events although did not alter the reported trends.

We used a combination of funnel plots and Egger's tests (Egger *et al.*, 1997) to assess potential publication bias. Visual inspection of the funnel plot suggested no systematic asymmetry in effect sizes (Fig. S1), a result also supported by the non-significance of Egger's tests (Table S3). To assess the sensitivity of our analysis to the use of Hedges' g , we also ran a parallel meta-analysis using the log-response ratio (LRR) as

the effect size. To calculate the LRR we divided values from impact treatments by those in the control treatments and took the logarithm of this number. We used the *escalc* function for this computation. Table S4 shows that our results are robust to the selection of the effect size, as the magnitude and direction of the effect sizes did not change significantly when comparing Hedges' *g* and LRR results.

All analyses and figures were performed using R v. 4.0.3 (R Core Team, 2020). Code and data are available at <https://doi.org/10.5281/zenodo.7004412>. We provide a completed PRISMA for Ecology and Evolutionary Biology (PRISMA-EcoEvo; O'Dea *et al.*, 2021) checklist in Table S5.

III. RESULTS

We analyzed 199 effect sizes for components of biodiversity (62 studies) and 100 effect sizes for ecosystem functions (26 studies) (see Table S4 for a summary of the effect sizes and their respective 95% credible intervals). The geographical distribution of the studies is shown in Fig. 1. Most studies were distributed in temperate and boreal regions in North America and Europe; very few were from tropical or arctic regions.

Our analysis of multiple components of river biodiversity revealed negative impacts of weather changes on species richness (Fig. 2). A univariate model for weather anomalies (trend *versus* event) revealed that these negative impacts were mainly due to extreme events [posterior mean of event: -1.08 (95% CI: -1.78 to -0.42), posterior mean of trend: 0.07 (95% CI: -0.73 to 0.9)]. The between-study heterogeneity variance of this model was estimated at $\tau = 0.75$ (95% CI: 0.06–1.5). A separate model for anomaly type showed that decreases in water flow caused the most dramatic impacts

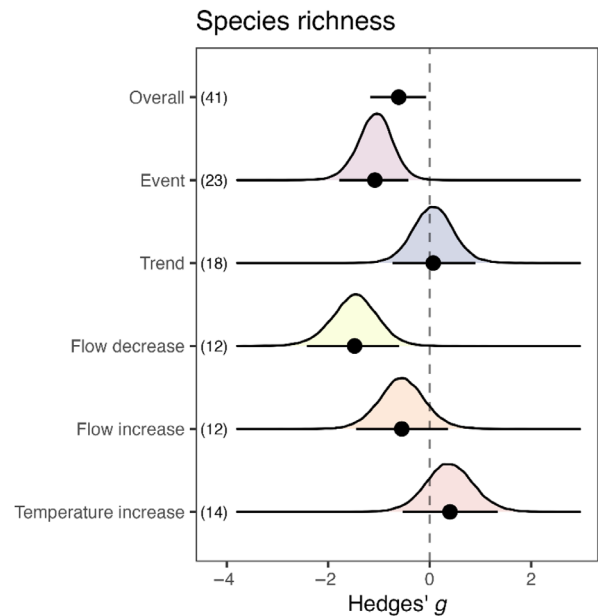


Fig. 2. Impacts of trend and event effects and anomaly type on species richness of river ecosystems. The distributions display the posterior probability of different effect sizes, dots corresponding to posterior means, and their horizontal bars to 95% credible intervals. The dashed line corresponds to an effect size of zero. Numbers in parentheses represent the sample size (i.e. number of effect sizes) for each predictor variable. Weather events, particularly flow decrease, had a significant impact on riverine species richness.

on species richness (posterior mean: -1.48, CI: -2.42 to -0.60). The between-study heterogeneity variance of this model was estimated at $\tau = 0.83$ (95% CI: 0.18–1.46).

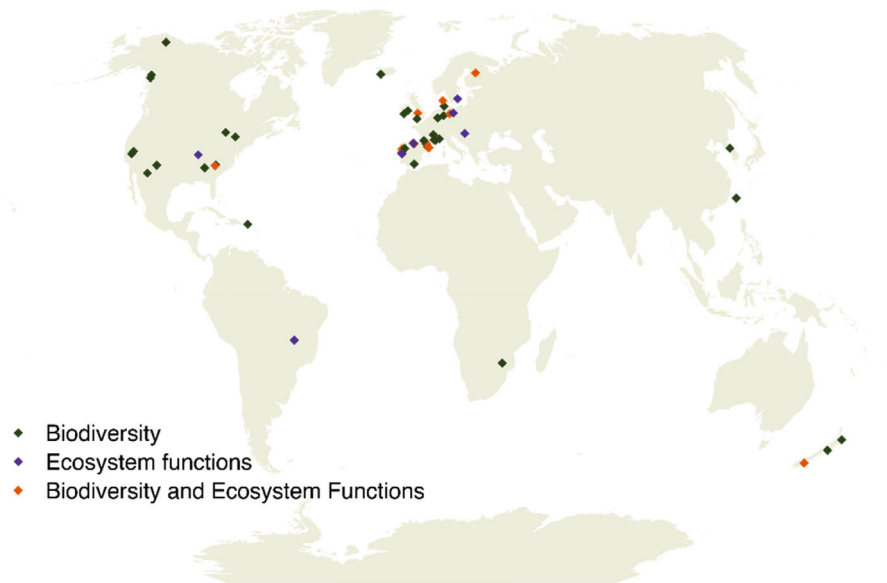


Fig. 1. Geographical distribution of the studies included in the meta-analysis. Different colours indicate whether studies contained data on biodiversity, ecosystem functions, or both.

Neither extreme increases in temperature nor water flow had detectable effects on species richness. In contrast to species richness, community density ($N = 85$) did not change consistently in response to trend or event effects (Table S4).

As was the case for species richness, community biomass showed an overall decrease in response to event effects and anomaly types (Fig. 3A, model's $\tau = -0.74$, 95%CI: -1.17 to -0.31). The decrease in community biomass was not significantly associated with trend effects (posterior mean: -0.62 , CI: -1.28 to 0.04), but the relationship was significant for event effects (posterior mean: -1.13 , CI: -1.84 to -0.41). A second model revealed that reduction in biomass is associated with increases in temperature and decreases in flow (Fig. 3A, model's $\tau = -1.04$, 95%CI: -1.89 to -0.19). However, the response of community biomass was not consistent across taxonomic groups. Independent models indicate that trend changes do not impair benthic algal

(biofilm) biomass (Fig. 3B), and that only extreme weather events affect fungal (posterior mean: -1.75 , CI: -3.41 to -0.09 ; model's $\tau = 1.08$, 95%CI: 0.04 – 2.96) (Fig. 3C) and invertebrate biomass (posterior mean: -1.46 , CI: -2.37 to -0.54 ; model's $\tau = 1.34$, 95%CI: 0.89 – 3.45) (Fig. 3D). We also found significant impacts of temperature increases and flow decreases on invertebrate biomass (model's $\tau = -1.48$, 95%CI: -2.53 to -0.43) (Fig. 3D).

Finally, our results did not show effects of anomaly type on most of the ecosystem functions (Fig. 4). Respiration (Fig. 4C) and organic matter decomposition (Fig. 4B) were not affected by either event or trend effects or anomaly type. The between-study heterogeneity variance of these models (type of effect: trend *versus* event) was estimated at $\tau = 0.98$ (95%CI: 0.06 – 2.20) for respiration; $\tau = 1.62$ (95%CI: 1.03 – 2.46) for decomposition; and $\tau = 0.83$ (95%CI: 0.03 – 2.61) for primary productivity. However, we found that

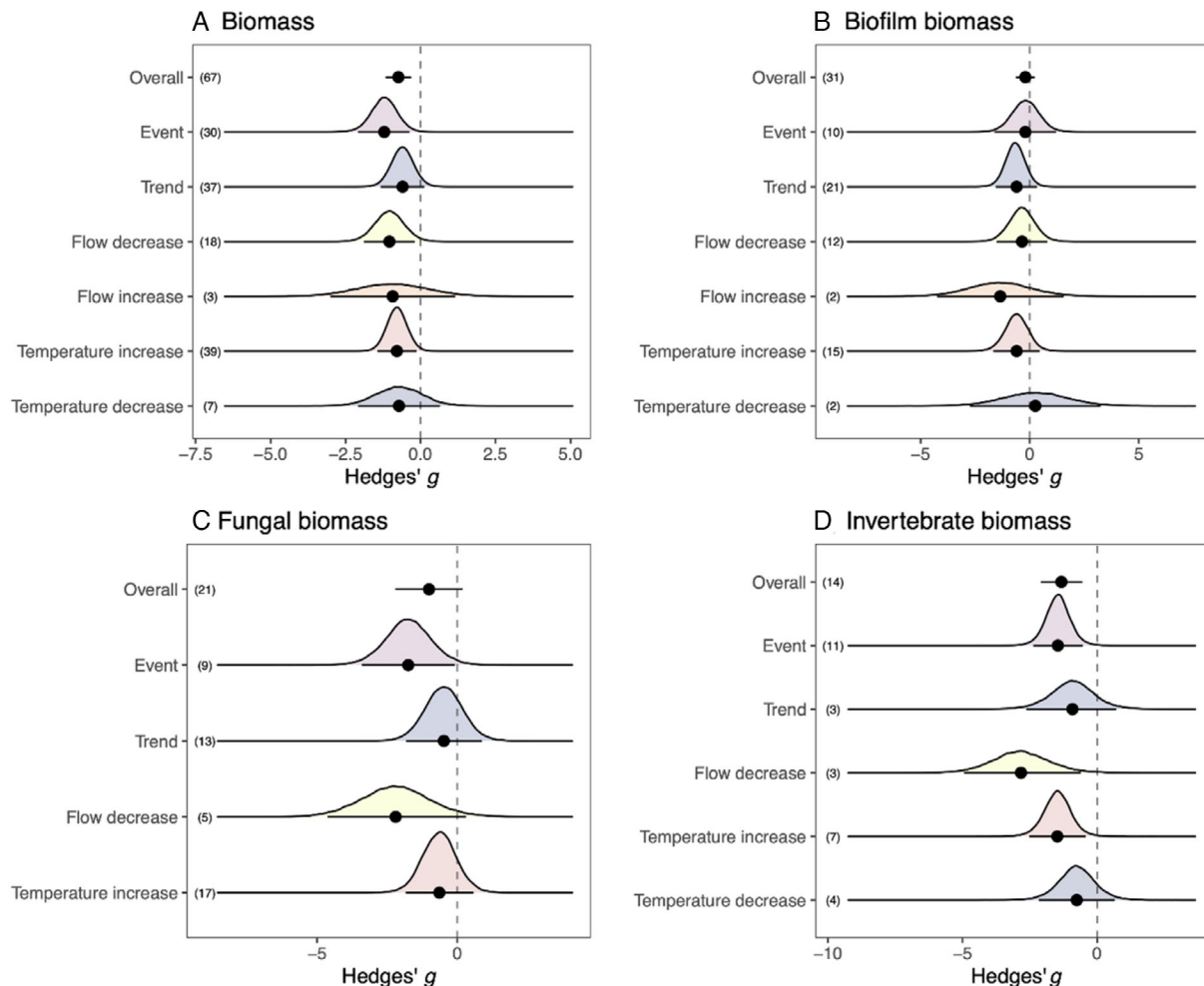


Fig. 3. Impacts of trend and event effects and anomaly type on the biomass of communities of river ecosystems (A), and on the biomass of biofilm (B), fungi (C) and invertebrate (D) communities. The distributions display the posterior probability of different effect sizes, with dots corresponding to posterior means and their horizontal bars to 95% credible intervals. The dashed line corresponds to an effect size of zero. Numbers in parentheses represent the sample size (i.e. number of effect sizes) for each predictor variable. Weather events (flow decrease) had a significant impact on biomass, mostly on that of invertebrates and fungi, but not on biofilm.

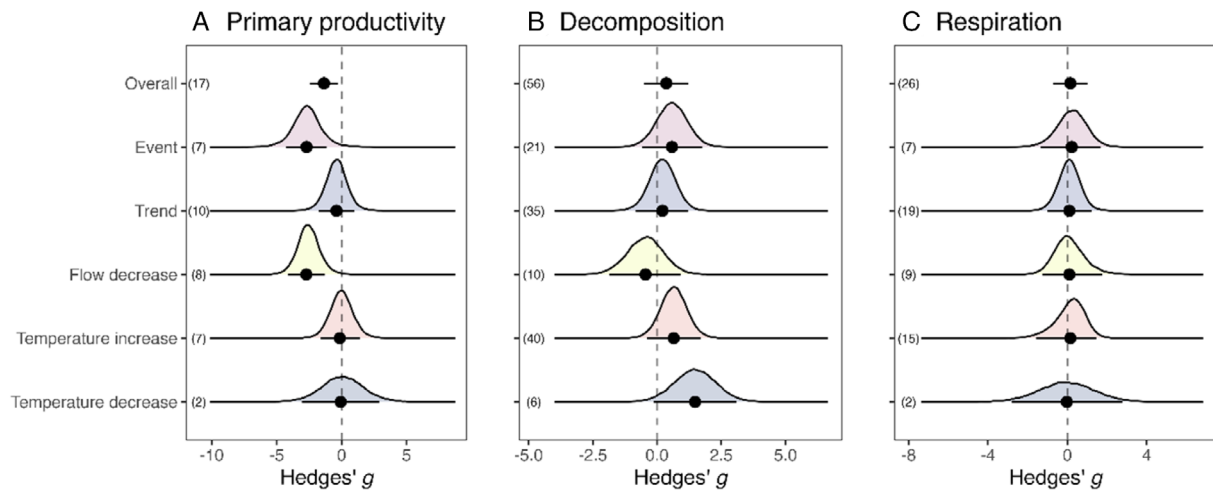


Fig. 4. Impacts of trend and event effects and anomaly type on ecosystem functions of rivers: (A) primary productivity, (B) decomposition, and (C) respiration. The distributions display the posterior probability of different effect sizes, with dots corresponding to posterior means, and their horizontal bars to 95% credible intervals. The dashed line corresponds to an effect size of zero. Numbers in parentheses represent the sample size (i.e. number of effect sizes) for each predictor variable. Only weather events, particularly flow decrease, had a significant effect, and only on primary productivity.

primary productivity was negatively affected by abrupt flow decreases (Fig. 4A, posterior mean: -2.73 , CI: -4.12 to -1.3). The between-study heterogeneity variance of these models (anomaly type) was estimated at $\tau = 1.05$ (95% CI: 0.05 – 2.73) for respiration; $\tau = 1.62$ (95% CI: 1.04 – 2.45) for decomposition; and $\tau = 0.88$ (95% CI: 0.04 – 2.46) for primary productivity.

IV. DISCUSSION

Ongoing changes in weather patterns may lead to transformative impacts on the biodiversity and ecosystem functions of river ecosystems across the globe. Here, we present a comprehensive meta-analysis showing that extreme weather events negatively affect the biodiversity of rivers, while of the ecosystem functions assessed, only primary productivity responded significantly, and only to weather events.

(1) Impacts on biodiversity of rivers

We found that extreme weather events had consistent, negative impacts on biodiversity (species richness and biomass) of river ecosystems. We determined that, on average, event effects on biodiversity were twice as strong as trend effects, which adheres to the definition of extreme event disturbances as localized, high-energy, rapid changes in environmental conditions (Peters *et al.*, 2011). Our results raise concerns about the future of riverine biodiversity since extreme events are increasingly frequent and will challenge the adaptation capacity of the biota (Ummerhofer & Meehl, 2017; Jentsch & White, 2019).

Event effects have driven considerable changes in a variety of ecosystems and biological compartments, spanning from soil microbiota (Fierer & Schimel, 2002), to meadow-dwelling insects (Piessens *et al.*, 2009), to fish foraging in coral reefs (Stuart-Smith *et al.*, 2021; Richardson *et al.*, 2018). In rivers, abrupt changes in water flow and temperature directly affect the habitat extent and suitability for organisms as they cause rapid variations in hydraulic and chemical conditions (Guse *et al.*, 2015; Petrovic *et al.*, 2011; Ponsati *et al.*, 2015). These variations challenge the adaptability of many species, with potential effects on the composition, diversity, and abundance of biological communities. Our results show that such effects differ for different biological compartments, with some being more vulnerable than others.

Our synthesis of the available evidence reveals that river biota do not exhibit consistent responses to extreme events. While the species richness and biomass of invertebrates were consistently negatively affected by water flow interruption, microbial communities showed inconsistent responses, ranging from non-significant effects for benthic algal (biofilm) biomass to decreases for fungal biomass. Rivers undergoing complete or abrupt flow interruptions experience dramatic declines in available habitat (Suren & Jowett, 2006; Pace, Bonada & Prat, 2013), leading to habitat fragmentation and to the prevalence of colonization–extinction processes. Only taxa with traits conferring resistance to low-flow conditions (usually associated with physical and chemical stressors, such as high temperatures, organic matter and fine sediment accumulations, and low dissolved oxygen levels) or prolonged droughts, will remain after an extreme event occurs (Townsend & Hildrew, 1994). The different responses obtained in our meta-analysis suggest that organisms with shorter life cycles (microbes) may resist and recover from

pulse disturbances (event effects) to a greater extent than organisms with longer lifespans. Shorter generation times, higher dispersal ability and greater heat, abrasion, and desiccation tolerance may confer microorganisms with a greater resistance to hydrological extremes (Sabater *et al.*, 2016; Chester & Robson, 2014).

By contrast with specific studies considered in our analysis (Gonçalves *et al.*, 2019; Romero *et al.*, 2019), we conclude that neither changes in water flow nor temperature affected biomass of microbes (except for fungi). The absence of detectable effects on microbial communities can be attributed to high heterogeneity among studies or perhaps to the inaccuracy of species richness as a measure of the impacts of environmental changes on river biodiversity (Hillebrand *et al.*, 2018). Losses of aquatic microbial species may favour the arrival of terrestrial species that are adapted to resist desiccation (Truchy *et al.*, 2020), which may alter the composition of the bacterial community, but not necessarily its richness (following a rather general pattern across ecosystems; Blowes *et al.*, 2019). Alternatively, the limited response of microbial biomass to hydrological disturbances suggests that other factors, such as the availability of resources or biological interactions, may enhance resistance (Krauss *et al.*, 2011). Water flow reduction, for example, does not reduce benthic algal biomass because lower flow primarily reduces grazing pressure (Truchy *et al.*, 2020).

Invertebrates are the biological group for which the most detailed evidence is available regarding responses to environmental effects. While several studies have determined that changes in the distribution, diversity and abundance of invertebrates are associated with long-term increases in water temperature or flow patterns (Durance & Ormerod, 2007; Domisch *et al.*, 2013), our analysis concludes that invertebrate richness and biomass are mostly sensitive to sudden (event) changes in water temperature and flow. Abrupt changes such as extreme droughts may induce effects on diversity (Bogan, Boersma & Lytle, 2015), mostly by affecting the most sensitive taxa (Piggot *et al.*, 2015a; Madji *et al.*, 2020). Ephemeroptera, Plecoptera and Trichoptera are the most affected groups of invertebrates, likely because they tend to be adapted to cold and highly oxygenated water, and they adapt poorly to warmer temperatures, lower dissolved oxygen levels, and shrinking waters (Cérèghino, Boutet & Lavandier, 1997; Tierno de Figueroa *et al.*, 2010). It has been observed that unseasonal or suprasonal flow interruptions (Lake, 2003) can cause unpredictable effects on macroinvertebrate richness and biomass, especially in permanent systems (Hill *et al.*, 2019). Several studies included in our meta-analysis show that flow interruptions may result in extensive loss of individuals and species (Calapez *et al.*, 2014; Dewson, James & Death, 2007), thereby directly affecting species richness and biomass. Direct effects of water flow interruption not only challenge the resistance of invertebrate communities, but also their recovery because the colonization rate of drifting and flying invertebrates is a function of the distance to drought refuges (Vander Vorste, Malard & Detry, 2015).

In contrast to interruptions in water flow, floods did not show consistent impacts on either species richness or biomass. While flood events may lead to losses of algae and macroinvertebrates *via* physical disturbance and washout (the scouring effect; Feeley *et al.*, 2012) and cause important changes in the geomorphological structure of rivers, they do not necessarily affect all taxonomic groups similarly (Piniewski *et al.*, 2017). This variability may reflect the differential ability of organisms to find shelter and the differential capacity of populations to recover quickly after floods subside (response diversity; Hershkovitz & Gasith, 2013). Our meta-analysis included several studies describing the effects of catastrophic floods (Tsai *et al.*, 2014; Feeley *et al.*, 2012; Foord & Fouché, 2016), which indeed reported large changes in the biomass of algae or invertebrates. Species loss of macroinvertebrates is most likely related to substratum movement and associated drift, and taxa inhabiting riffle areas (e.g. blackflies) are the most affected (Milner *et al.*, 2013). However, with certain exceptions (e.g. Hynes, 1970; Woodward *et al.*, 2015), studies monitoring the responses of invertebrate communities after floods have shown rapid invertebrate recovery (Herbst *et al.*, 2019; Baillie *et al.*, 2020), with an initial decline in abundance usually followed by a rapid increase in both abundance and species richness. Moderate floods may even enhance the mobility of nutrients and sediment, and the complexity of the river habitat (Death, Fuller & Macklin, 2015). Floods may therefore confer a competitive advantage to invertebrates with rapid development of aerial stages, asynchronous egg hatching, and synchronized metamorphosis with flood timing (Lytle & Poff, 2004).

Compared to water flow, we found that temperature changes induced few direct and indirect effects on the biomass of stream biota. Moderate short-term warming has not been found to cause substantial effects on the biomass of biofilm communities (Romero *et al.*, 2019), but sustained warming may increase the functional richness and diversity of benthic microbial communities (Ylla, Canhoto & Román, 2014). Warming generally enhances microbial activity (Diaz Villanueva, Albariño & Canhoto, 2011) but may cause changes in resource acquisition (Romero *et al.*, 2019). In macro-organisms, warming may produce direct effects on the metabolism, leading to increased growth rates and smaller size at maturity. Indirect effects on macro-organism survival occur through changes in the availability and quality of basal resources (Piggot *et al.*, 2015b; Hogg & Williams, 1996), which may account for our observed decrease in invertebrate biomass in response to warming (Fig. 3D).

(2) Impacts on ecosystem functions of rivers

Contrasting with responses in biodiversity, the ecosystem functions of rivers did not exhibit consistent, negative responses to weather variability. Only primary productivity exhibited a negative response to event effects, largely due to a negative response to extreme water flow decreases. Neither

respiration nor organic matter decomposition were affected by trend or event effects.

This synthesis of available evidence reveals that extreme water flow reduction consistently reduces primary productivity. Low flow, particularly during certain periods (e.g. summer), consistently decreases stream width and water velocity, favours higher water temperature, and reduces nutrient uptake (Riis *et al.*, 2017). The physical constraints imposed by low water velocity (and associated higher thickness of the boundary layer over the stream bottom) have been found to lead to consistent decreases in net and gross primary production (Riis *et al.*, 2017; Arias-Font *et al.*, 2021), moving the balance from autotrophic to heterotrophic (Acuña *et al.*, 2015; Romero *et al.*, 2019). This shift towards heterotrophy is probably due to collapse of the photosynthetic capacity of primary producers under dry conditions (Colls *et al.*, 2021).

The lack of response of respiration and decomposition to trend or event effects in our meta-analysis does not support results of previous case studies showing that extreme events affect organic matter decomposition in river ecosystems. A recent study showed that the effects of drying on shredders did not affect leaf litter decomposition (Carey, Chester & Robson, 2021), highlighting the variable or uncertain outcomes of interactions among climate, water quality, and decomposers (Bernabé *et al.*, 2018). The response of microbial decomposition to changes in water stress is highly context dependent, reflecting differential responses of microbial communities to temperature, nutrient, and oxygen levels (Duarte *et al.*, 2017). Our meta-analysis indicates that extreme events can reduce fungal biomass, which is associated with decomposing substrates, while decomposition itself remained unaffected. Gonçalves *et al.* (2019) showed that fungal biomass and diversity decreased after experimentally reducing water flow by 74–88%, but that ecosystem functions were maintained, suggesting that fungal communities have high functional redundancy. Similarly, Arias-Real *et al.* (2022) found that a reduction in species richness did not alter decomposition rates in fungal communities with initial higher richness. Species-rich communities exhibit a wider range of ecological and functional responses to stressors than less-diverse communities, making them more resistant to disturbances (McLean *et al.*, 2019). Overall, the apparent discrepancy between biodiversity and functional responses of river ecosystems to hydrological and climate trends and events highlights the role that functional redundancy (Biggs *et al.*, 2020) may have on conserving the provisioning of ecological functions.

(3) Caveats of the analysis

While our meta-analysis revealed stronger effects from extreme weather events, we recognize that our results may reflect limitations associated with the distribution, type, and number of studies. We found few studies from Asia, Africa, and South America, whose river ecosystems show specific differences (e.g. Dudgeon, 2008; Petsch *et al.*, 2020; González-Trujillo *et al.*, 2021) compared with the temperate ecosystems

that comprise most effect sizes in our study. Secondly, only a small number of studies provided initial conditions to be compared with data after disturbances (Peters *et al.*, 2011). This is an essential requirement for quantifying effect sizes. Due to this constraint, we included studies from a variety of contexts, ranging from field observations, to manipulative field studies, to experimental studies in the laboratory. Including this variety of studies to enable sufficient statistical power may, however, restrict the transferability of our results to real-world ecosystems, as the magnitude of climate change treatments frequently exceeds model-based projections (Korell *et al.*, 2020). Thirdly, the data gaps for ecosystem functions, which are pervasive (von Schiller *et al.*, 2017), did not allow us to define the temporal frame or period under which trend or event effects are more (or less) damaging (Trisos, Merow & Pigot, 2020). It should be kept in mind that most studies conducted so far on ecosystem functions have been performed under controlled conditions, at relatively short spatial and temporal scales (Estes *et al.*, 2018) and exclude biotic components that may also contribute to ecosystem functions (e.g. detritivores in decomposition studies and grazers in primary production studies).

Finally, the low sample size also affected our ability to quantify precisely the impacts of weather anomalies, particularly for groups such as fish or bacteria. There is need for a larger number of studies to reduce between-studies heterogeneity (our measured τ) and provide more accurate estimates. We dealt with imperfect data availability by conducting a Bayesian meta-analysis, which allows direct modelling of the uncertainty of τ estimates and improves estimations of the pooled effects when the number of included studies is small (McNeish, 2016). Bayesian methods produce full posterior distributions that allow comparison of the whole spectrum of impact levels caused by trend or event effects.

Despite these caveats, our meta-analysis is the most comprehensive to date on the impacts of hydrology and climate trends and events on the biodiversity and ecosystem functions of river ecosystems. Future research should aim to expand how the impacts of trend and event effects on river ecosystems are quantified in terms of biodiversity or ecosystem functions in order to test the differential effects of extreme stressors and their consequences for the future of rivers. We call on future investigators to measure the impacts of statistically unusual events (i.e. above the 99th percentile) using standardized protocols.

V. CONCLUSIONS

- (1) Our study provides insights into the impacts of extreme weather events on the maintenance of biodiversity and ecosystem functions in river ecosystems.
- (2) We found evidence that substantial changes may occur at population and community levels, but mostly for larger organisms such as invertebrates.

- (3) Even though impacts on ecosystem functions are less evident, primary productivity was particularly impacted by extreme conditions.
- (4) Strong, negative impacts of certain types of anomalies, especially water flow interruption, cause effects that may shift biodiversity and (at least some) ecosystem functions irreversibly beyond their dynamic stable states (Trisos *et al.*, 2020).
- (5) Evidence that weather extremes may have long-lasting impacts on the biodiversity and ecosystem functioning of river ecosystems already exists. The Millennium drought in Australia (1997–2009) led to some rivers being unable to recover to pre-drought flow regimes (Peterson *et al.*, 2021), with these river ecosystems providing examples of ‘no turning back’ in response to weather extremes that cause irreversible effects.

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VII. AUTHOR CONTRIBUTIONS

S. S. and J. L.-D. designed the study. S. S., J. L.-D., A. F., L. J. and N. P. extracted data from the text, tables, figures, or supplementary information in the reviewed papers. J. D. G.-T. performed the statistical analyses. S. S. and J. D. G.-T. led the writing, and all other authors discussed and contributed to revisions.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Search terms used in the literature search for studies used in our meta-analysis.

Appendix S2. PRISMA diagram for the literature search.

Table S1. List of moderators used in statistical models.

Table S2. Identification of the most appropriate random effects structure by leave-one-out cross-validation.

Fig. S1. Funnel plots of effect sizes (Hedges' g) plotted against the inverse standard error of sampling variances.

Table S3. Results of the Egger's tests assessing publication bias.

Table S4. Mean effect sizes (Hedges' g and log response ratio) and 95% credible intervals for biodiversity and ecosystem function response variables.

Table S5. Completed PRISMA ECO-EVO checklist.

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